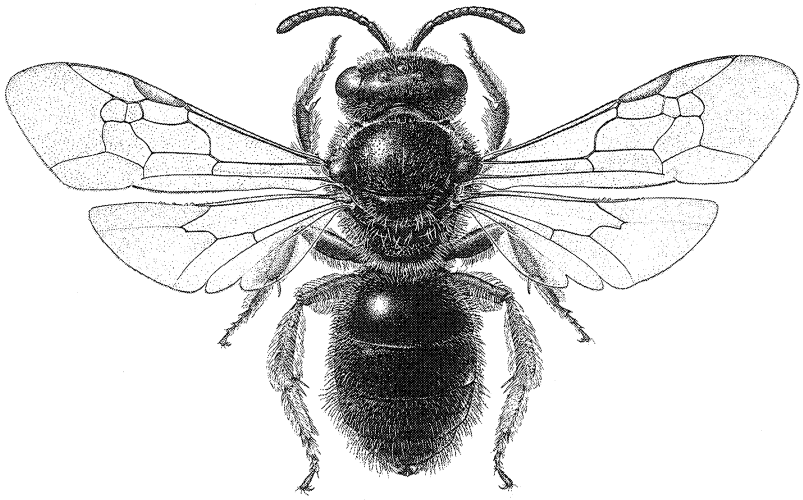
The Bee Genera of North and Central America (Hymenoptera: Apoidea)



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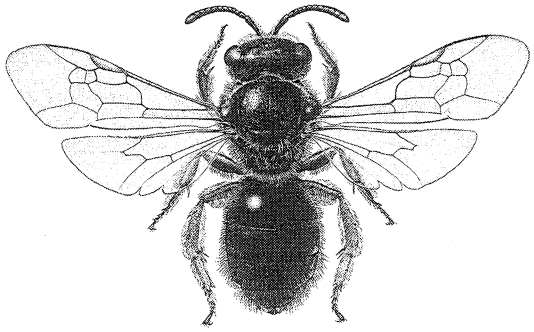
Introduction



For years entomologists, ecologists, botanists interested in pollination problems, and others have urged the preparation of a key to facilitate identification of genera of bees in North and Central America. Bee specialists, finding such identification relatively easy for them, have not hitherto provided such a key, although certain regional accounts and keys exist: Michener (1944—key to genera found north of Mexico); Mitchell (1960, 1962—eastern United States and Canada); Stephen, Bohart, and Torchio (1969—northwestern United States); Michener (1954a—Panama); and Ayala (1988—Chamela, Mexico).

As a step to promote studies of Mexican bees in Mexico, the Programa Cooperativo sobre la Apifauna Mexicana (PCAM) was initiated in 1985. An obvious need was a key for identification of Mexican genera for persons not thoroughly familiar with bees, and we undertook to prepare one. It soon became clear that few genera are found in the United States and Canada that do not also occur, or probably occur, in Mexico. The list of such genera is as follows: *Cemolobus, Epeoloides, Macropis*. By adding these genera to the key to Mexican genera, we expanded the area of coverage to the whole of North America.

A few additional genera, not known from Mexico, occur in Central America (Panama to Guatemala) and the Antilles. We have added them to the key, so that one should be able to identify to genus any bee known from north of the Colombia-Panama border. A total of 169 genera are recognized; probably additional South American genera will be found with more collecting in Central America and even southern Mexico. The key should be useful, however, throughout moist tropical America—for example, in the Amazon Valley. On the other hand, temperate South America, the Andes, and xeric areas like northeastern Brazil have quite different bee faunas. To encourage study of bees in Latin America, we have included Spanish translations of the keys.

We follow current custom in recognizing several families of bees, most of them divided into subfamilies and tribes. In view of the close relationship of bees and sphe-

coid wasps, we place both groups in a single superfamily (to be called Apoidea; see Michener 1986a), with all bees in an informal group called the apiformes (Brothers 1975:587). One of us (CDM) is in the midst of a restudy of the higher classification of bees (see Appendix D); we have been conservative, therefore, in proposing major changes that might turn out to be premature.

In a few cases, nevertheless, we have made minor classificatory changes or accepted a view that may have been published but is not yet widely followed. Such matters are explained briefly in "Notes on the Genera," and a list of names having a new or not generally accepted status is provided in the section "Classificatory and Nomenclatural Changes."

The classificatory changes are generally intended to make genera somehow equivalent in various groups of bees. Although many people agree that this is a desirable goal, there is no practical and objective way, nor widely accepted criterion, for measuring equivalence in a large study such as this. Nevertheless one can subjectively say that the genera differ by less conspicuous and less numerous features—and are therefore more difficult to distinguish—in some groups, such as Eucerini and Augochlorini, than in other groups. It has not been practical to modify this situation here. We have in general taken the view, widespread and old but not universal among bee specialists, that a moderate number of large, readily distinguishable genera is preferable to a large number of small genera. Thus genera like *Culex, Aedes, Drosophila,* and *Andrena* mean something to many biologists. Each such genus could be split merely by raising subgenera to generic status, but usefulness to a broad audience argues against that action.

As a tool for practical identification, the keys and accompanying "Notes on the Genera" are not the places for cladistic or other major new classificatory work. As indicated above, such studies are going on. For the present, we have taken the genera as they stand (except for a few changes that seem needed) and tried to make them relatively easily identifiable. Some are almost surely paraphyletic, which for some workers but not others necessitates a change. In the absence of soundly based phylogenies for most groups, we have delayed discussion of such problems.

Our objective here being to facilitate generic identification, we have not attempted to provide an introduction to the many studies on nesting behavior and floral biology of bees. For an overview of such topics, we recommend O'Toole and Raw (1991). For references to the primary literature on the taxonomy, behavior, and ecology of bees north of Mexico, see Hurd (1979); primary literature for the family Halictidae of the Western Hemisphere can be found in Moure and Hurd (1987). Roubik (1989) provides a recent account of tropical bee biology. All these sources provide references on social behavior and can be supplemented by Michener (1974) and chapters in Engels (1990). References to works on bee larvae are provided by McGinley (1989).

All three authors have used and improved all parts of this work. CDM prepared the original versions of all the keys and "Notes on the Genera" and arranged for most of the wing drawings. RJM and BND prepared or supervised preparation of nearly all the other drawings and photographs, contributed to the improvement of the keys, and were entirely responsible for arranging the text and illustrations and correlating the interlocking parts of the work.

How to Recognize a Bee

Bees constitute a monophyletic group of aculeate Hymenoptera (bees, ants, and wasps). The superfamily Apoidea (formerly called Sphecoidea, but see Michener 1986a), which includes bees and sphecoid wasps, can be recognized by a number of characters, of which the following two are the strongest: (1) The pronotal lobe [Fig. 13] is distinct but rather small, usually well separated from and below the tegula. (2) The pronotum is extended ventrolaterally as processes that encircle or nearly encircle the thorax behind the forecoxae.

The Apoidea is divisible into two groups: the sphecoid wasps, or spheciformes, and the bees, or apiformes (Brothers 1975). The bees, which are believed to have arisen from the paraphyletic spheciformes, have abandoned the ancestral predatory habit of feeding larvae on insect or spider prey. Instead they use pollen as the principal protein source for their larvae; the pollen is mixed with nectar or honey, or sometimes with floral oils or with

glandular products of adults. (Although some meliponine bees use carrion as a protein source, and some bees eat eggs of others, bees are almost exclusively phytophagous.)

In general, bees are more robust and hairy than wasps, but some bees (e.g., *Hylaeus, Nomada*) are slender, sparsely haired, and sometimes wasplike even in coloration. Morphological characters of the apiformes include the following: (1) Some of the hairs are plumose or branched. (In spheciformes they are simple.) Commonly, branched hairs of bees are visible at moderate magnification on various parts of the body and legs, but sometimes they are limited to a few areas (e.g., the propodeum) [Figs. 13 and 14] and can be difficult to see. (2) The hind basitarsus is broader than the subsequent segments of the tarsus and is commonly flattened [Fig. 11]; it does not have a gentle concavity on one side facing the tibial spurs and forming a cleaning structure, or strigilis. (In the spheciformes, the first and second tarsal segments are similar in width, and one side of the first forms, with the tibial spurs, a strigilis used in cleaning the opposite hind leg.)

A conveniently visible character that easily distinguishes nearly all bees from most sphecoid wasps is the possession by the wasps of golden or silvery hairs on the lower face, so that the face glitters in the light. Bees almost never have the same characteristic, because their hairs are duller, often erect, often plumose, or largely absent. This feature is especially useful in distinguishing small, wasplike bees such as *Hylaeus* from similar-looking pemphredonine wasps.

Collection and Preservation of Specimens

Until one is thoroughly familiar with the habitus and behavior of the bees in a particular area, it is difficult to identify many bees with certainty, even to the generic level, without collecting specimens and examining them microscopically or at least with a hand lens. Therefore, capturing and preserving specimens is essential for studies of bee ecology, pollination, and so forth. Standard entomological techniques of capturing with an insect net and using a killing jar or tube with cyanide or ethyl acetate are recommended. Because many bees are hairy, it is important to keep such jars or tubes dry; excess moisture or excess ethyl acetate mats the hairs, thus changing the appearance of the specimens and making it difficult to see important characters. Several hours in cyanide vapor in hot weather changes yellow integumental colors to red. To keep specimens dry and prevent such undesirable color changes, one should take them out of killing tubes or jars after they are dead and place them in pillboxes. Moisture will condense inside of closed vials, resulting in matted hairs; such vials or other sealed containers therefore should not replace pillboxes, although vials with loose cotton plugs will suffice for small numbers of specimens.

For easy handling as well as for long-term preservation, it is best to pin specimens a few hours after they are killed, using standard entomological procedures (cf. Oman and Cushmann 1946; Gibson 1960; Steyskal, Murphy, and Hoover 1986; Borror, De Long, and Triplehorn 1981). For example, small specimens whose thoraces would be disrupted by an insect pin should be glued to paper "points" or glued directly by the right side of the thorax to the insect pin at an appropriate height. (Have the glue encircle the pin to avoid loss later.) Steel minuten pins can be used instead of paper points for fresh material but not for dried material, which will not adhere to such pins. If it is impractical to pin specimens while they are still soft, they can be allowed to dry in the pillboxes or between layers of Cellucotton. Mild oven drying in the moist tropics helps to prevent mold. Later the specimens can be relaxed in a humid chamber until they are no longer brittle; then they can be pinned. Do not forget to label the pinned specimens.

For short-haired bees, like most stingless bees (Meliponinae), a satisfactory alternative is to put the bees directly from the net into vials of alcohol. They can then be pinned whenever convenient. For long-haired bees, the result of this procedure is matted hairs unless great care is exercised at the time of pinning to blow the hairs as they dry; this usually works well only if drying is from some fast-evaporating solvent rather than from alcohol. If available, critical-point drying provides good results. Long-term preservation in alcohol can be improved by freezing (L. Masner, pers. comm. 1987).

For many purposes, such as use of "Key to the Families," mouthparts should be extended. It is therefore desirable to open the mandibles and extend the proboscis for at least one specimen of each species while it is still soft.

Specimens killed with ethyl acetate commonly die with the mouthparts extended or are so relaxed that it is easy to extend them.

Once the specimens are on pins, it is easy to examine them from all angles under a microscope in order to see the characters used in identification. If unpinned material is used, such work is much more difficult and usually results in breakage if the specimens are dry and brittle.

It is surprisingly easy to ship dry pinned specimens through the mail—to have identifications verified, for example. An interior box containing the firmly pinned specimens should be surrounded by at least 5 cm of soft packing material in a sturdy outer box. However, persons not familiar with entomologists' methods should seek advice before committing a valuable lot of specimens to the post office.

Use of Data on Floral Visitations

Persons interested in floral biology, potential isolating mechanisms in plants, and the like frequently study insect visitors to flowers as possible pollinators. One must remember that every insect has to sit somewhere. Therefore, the mere presence of an insect, even of a bee, on a flower does not indicate a significant role in floral biology. For many flowers, great patience is needed to see and capture the principal pollinators. Moreover, plant populations probably often occur for at least a few years in habitats where the evolutionarily important pollinators are absent; studies of pollinators of a plant at diverse sites are therefore necessary for an adequate understanding of plant–pollinator relationships. Recognition of morphospecies in the field is often extremely difficult; therefore, substantial series of insect floral visitors must be collected. Although it is often of interest to ecologists as well as entomologists to record bees that collect pollen from a diversity of floral species (polylectic bees), it is also of great interest to investigate floral relationships of pollen specialists (oligolectic and monolectic bees), those that collect from related flowers or from a single species.

Even if bees are seen going from flower to flower and collecting pollen, they may or may not be significant pollinating agents. Minute bees, for example, may collect pollen from long stamens or take nectar from nectaries without going near the stigma. Such bees are thieves, parasites from the floral standpoint. They are highly interesting to us as students of bees but are of no significance for pollination biology. So observations of floral visitors, particularly on large flowers or on flowers with long stamens, need to include behavioral information that will help to distinguish pollinators from pollen thieves. Of course, there are numerous intermediates between these categories. A "thief" may sometimes contact a stigma, and pollinating bees are collecting pollen for their own food or that of their young—the amount they lose on stigmatic surfaces will depend on their behavior as well as on characteristics of the pollen and of the receptive surfaces.

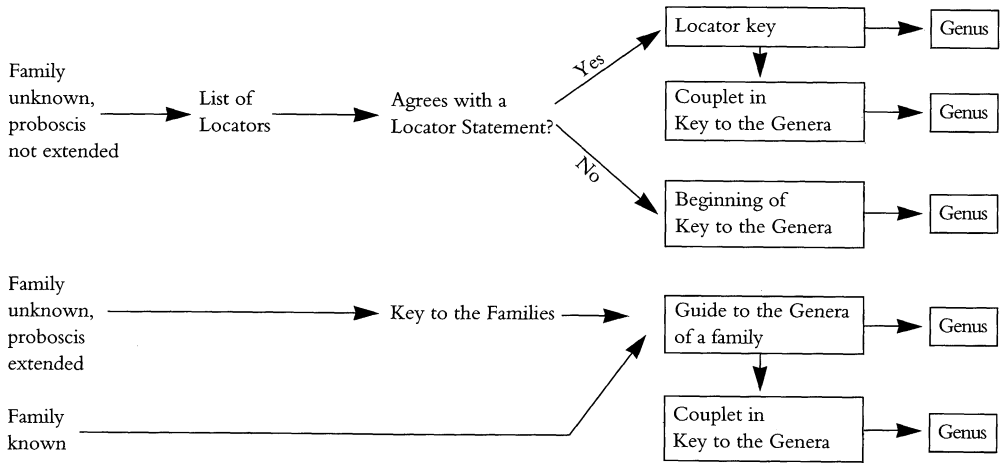


Fig. 1. Alternative routes to the identification of a specimen using the keys in this book.